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(NASA-CR-160397) PHOTOSYNTHETIC CARBON
REDUCTION BY SEAGRASSES EXPOSED TO
ULTRAVIOLET A RADIATION Final Report
(Florida Inst. of Tech.) 38 p HC A03/MF A01

N80-13757

Unclas
CSCL 06C G3/51 46255

160397



Florida Institute of Technology

Melbourne, Florida 32901

PHOTOSYNTHETIC CARBON REDUCTION
BY SEAGRASSES EXPOSED
TO ULTRAVIOLET A RADIATION

FINAL TECHNICAL REPORT

School of
Science and
Engineering



Submitted to
National Aeronautics and Space Administration
Lyndon B. Johnson Space Center
Technical Library Branch
Attention: Retha Shirkey, JM6
Houston, TX 77058

Contract No. NAS 9-15846

Photosynthetic Carbon Reduction
by Seagrasses Exposed
to Ultraviolet-A Radiation

Final Technical Report

Submitted by
Florida Institute of Technology
Melbourne, Florida 32901
(305) 723-3701

15 September 1979

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FOREWORD

This investigation was conducted in the Biological Sciences Department of Florida Institute of Technology, under the direction of Dr. Gary N. Wells. The program was funded by the Medical Sciences Division, with Dr. D. S. Nachtwey providing program direction.

While all members of the Florida Institute of Technology project team contributed to all portions of the study through frequent meetings to assure good coordination, the primary responsibility for Phase I and Phase II investigations belong to Mr. Robert Trocine and Mr. John D. Rice. Others who provided technical assistance include Mr. Bill Aspden and Mrs. Kathy Austin.

The author acknowledge the support throughout the program of Dr. G. C. Webster, Head of the Department of Biological Sciences, Mrs. Carolyn Sorrell, Departmental Secretary, and Miss Dee Dee Looney for typing the report manuscript.

INTRODUCTION

A decrease in the atmospheric ozone layer is considered to be one consequence of continued release of NO_x and chlorofluoromethanes into the environment, as well as the impending space shuttle program. A direct result of this ozone loss would be an increase in the total ultraviolet radiation reaching the Earth's surface. In all but the most drastic situations the increase in ultraviolet radiation would be limited to the portion of the spectrum referred to as ultraviolet-B (UV-B), wavelengths from 280 nm to 315 nm. A previous study by this laboratory (NAS 9-15516) examined the effects of an increased UV-B regime upon three seagrasses abundant in the intercoastal waters of the Florida east coast: Halophila engelmannii, Halodule wrightii, and Syringodium filiforme.

To summarize the results of that study, all three seagrasses show a decrease in photosynthetic activity as a function of increased UV-B irradiation. Halodule wrightii was the only seagrass studied which had an intrinsic tolerance to UV-B. This species was also the only seagrass to show any evidence of a photorepair mechanism which could at least attenuate the rate of UV-B induced, photosynthetic damage. Both tolerance and repair varied as a function of UV-B dose rate and total dosage. Syringodium filiforme showed a continual decrease in photosynthetic activity as the total dosage of UV-B presented to the seagrass increased. This species apparently relied on its morphology (a thick epidermis and concentration of photosynthetic apparatus in the core tissues) to prevent serious UV-B induced damage. Finally,

Halophila engelmannii was the most sensitive seagrass to UV-B irradiation, possessing no protective or photorepair mechanism. The restriction of this species to habitats at greater depth or of lower light penetration by more competitive species apparently serves to protect Halophila from UV-B exposure.

Some observations obtained while studying the effects of UV-B on the photosynthesis of seagrasses were unexpected, and posed more questions than could be answered in a short period of time. In this present study our laboratory has attempted to gather information on seagrass sensitivity to UV-A (wavelengths from 315-400 nm) and answer the following questions:

1. Are the seagrasses Halophila engelmannii, Halodule wrightii, and Syringodium filiforme intrinsically sensitive to UV-A?
2. If a seagrass is sensitive to UV-A, how is this sensitivity affected at different photosynthetically active radiation (PAR) intensities; i.e. does a particular intensity or range of PAR intensities cause a sensitization of the seagrass to UV-A resulting in photosynthetic inhibition?

The answers to these questions will in turn help to answer a third question; is UV-A or UV-B currently of greater environmental consequence in terms of seagrass distribution and abundance? Of interest is the fact that a decrease in the atmospheric ozone layer's thickness would not significantly affect the amount of UV-A reaching the Earth's surface while UV-B penetration would increase with the ozone loss.

Levels of UV-A at the surface are primarily a function of solar phenomena and transient atmospheric effects.

METHODS AND MATERIALS

A. Seagrass collection and saline analysis.

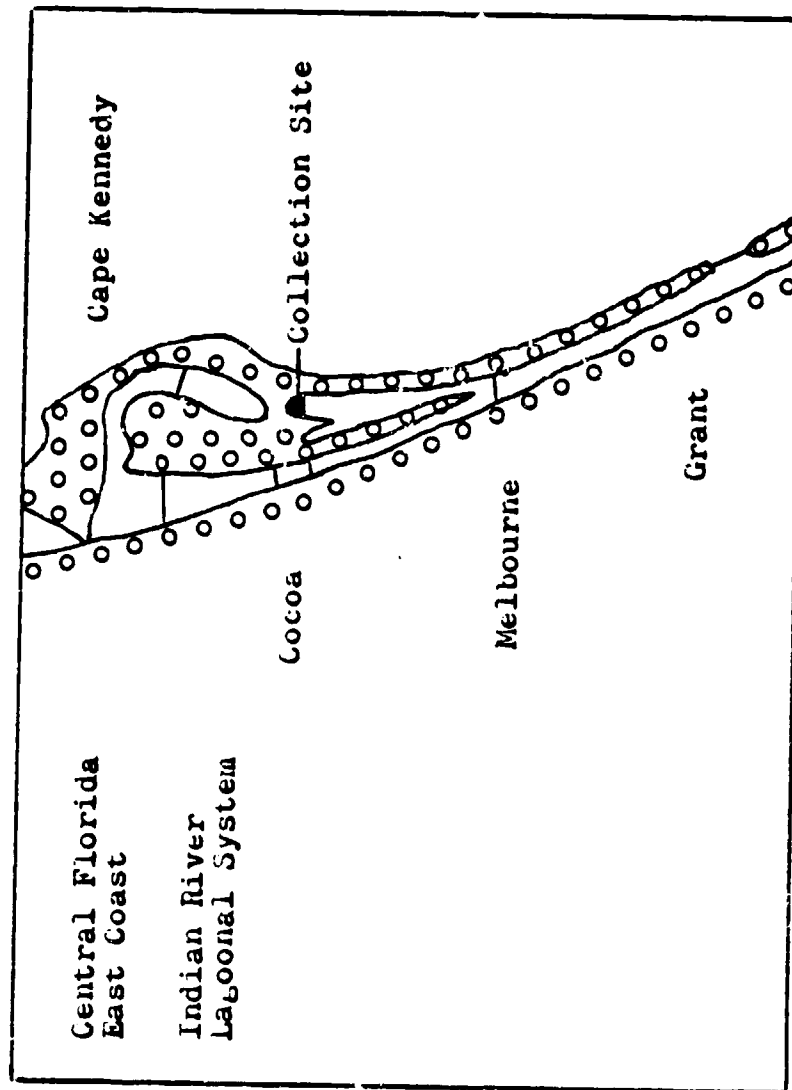
The three seagrasses were collected from a single site (Figure 1) the morning of the experiment and transported to the laboratory in water obtained at the site. Samples of each seagrass (about 75 mg) were cleaned of epiphytes, their fresh weights determined, and placed in petri plates containing approximately 50 ml of filter sterilized sea water (FSSW). Three sets of samples (from each seagrass) were prepared: one set of controls to receive ambient laboratory PAR (approximately $15 \mu\text{E}/\text{m}^2/\text{sec}$) alone, another set to receive only UV-A, and a third set to receive both UV-A and PAR. Visual uniformity of sample was stressed across the test period.

Fresh seawater was obtained for each experiment and sterilized by Buchner filtration with Whatman #4 filter paper followed by Millipore filtration (pore size of $0.45 \mu\text{m}$). Salinity was determined from the refractive index using an American Optical T/C Refractometer and the equation:

$$\text{Salinity (ppt)} = (\text{R.I.} - 1.3330) \times 0.54 \times 10,000$$

Total alkalinity, carbonate alkalinity, total CO_2 (all forms), $[\text{HCO}_3^-]$, and $[\text{CO}_3^{2-}]$ were determined as described by Strickland and Parsons (1). From these data the available μg ^{12}C in the FSSW was calculated for the interpretation photosynthetic ^{14}C incorporation studies (Methods, section C). Dissolved oxygen was measured using the Winkler method (2).

Figure 1. Seagrass collection site, Indian River lagoonal system (closed point, collection site).



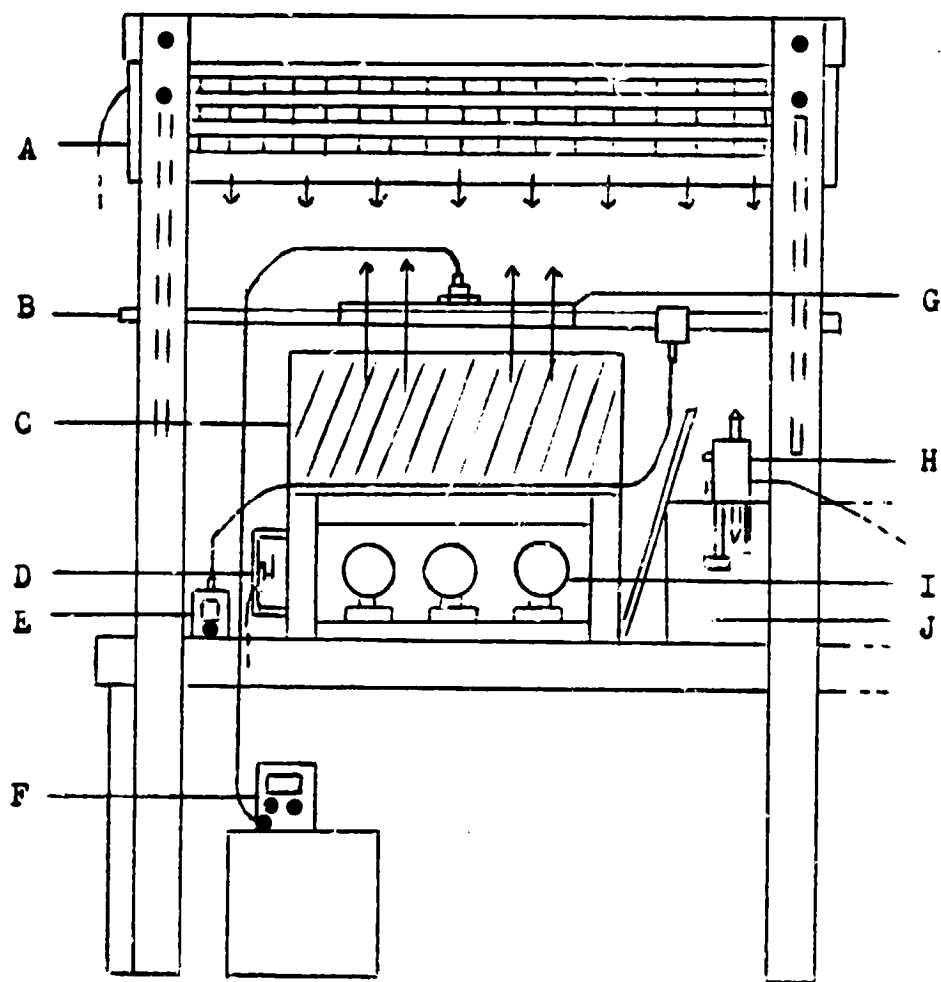
B. Irradiation studies.

Ultraviolet radiation was provided by a bank of six Westinghouse FS-40 fluorescent sun lamps (Figure 2). An UV-B dose rate of 10 CPM was used in all irradiation experiments. Six 300 watt white light bulbs were used to generate PAR with a Powerstat Variable Autotransformer (Superior Electric Co., type 116B) to adjust the light intensity from 0-700 $\mu\text{E}/\text{m}^2/\text{sec}$. After leaf tissue samples were prepared, one pair of each seagrass was placed on an irradiation grid of monofilament nylon, ultraviolet irradiation from above was limited to UV-A by placing a film of Mylar (10 mil, Dupont) over the samples while PAR was provided from below.

Irradiation was allowed to proceed until an UV-B dosage of 2000 counts was reached, monitored by a Sunburn Ultraviolet Meter (Solar Light Company) with a remote sensor mounted in the test platform. A Kodacel film (5 mil, Eastman Kodak) was placed over the sensor; this film allowed both UV-A and UV-B to penetrate but the sensor is only responsive to UV-B. Use of a spectral radiometer would have been preferred to allow calibration of the sensor and actual measurement of UV-A dosages experienced, unfortunately this equipment was unavailable. White light intensities were set and monitored with a Licor quantum/radiometer/photometer (Model LI-185A).

Once a UV-B dosage of 2000 counts was reached, the samples were placed in the dark until their photosynthetic rate at 30°C and 700 $\mu\text{E}/\text{m}^2/\text{sec}$ could be determined (Methods, section C). Irradiation control samples of each seagrass were then placed upon the test platform and

Figure 2. Ultraviolet and PAR irradiation apparatus; A) FS-40 fluorescent sun lamps; B) adjustable test platform; C) heat sink; D) fan; E) Sunburn Ultraviolet Meter; F) Licor photometer; G) plexiglass window; H) water pump; I) PAR light bank; J) cooling tank.



exposed to UV-A (in the absence of PAR) until 2000 counts of UV-B were again received. At this point irradiation was terminated, samples placed in the dark, and photosynthetic rate determined as before.

C. Photosynthetic rate determination.

Incorporation of [^{14}C] sodium bicarbonate into acid-stable intermediates was used to determine photosynthetic rates following exposure to UV-A in the presence or absence of PAR. After irradiation, leaf tissues were placed in 100 ml beakers containing 200 ml FSSE and equilibrated at $700 \mu\text{E}/\text{m}^2/\text{sec}$ and 30°C for 10 minutes in a water-cooled incorporation chamber similar to Figure 2. After equilibration, the leaf tissues were transferred to 100 ml beakers containing 5 ml fresh FSSW, returned to the chamber, and 15 μl of [^{14}C] sodium bicarbonate (1 mCi/ml, 50 mCi/m mole) was added to each of the samples. Following an incorporation period of 15 minutes the leaf tissue was removed, washed thoroughly with deionized water (D.I. water) and homogenized in glass Ten-Broeck homogenizers containing 1 ml of hot methanol. The homogenates were clarified by centrifugation at 2300 RPM for 5 minutes in 15 ml conical tubes and methanol soluble fractions (MSF) transferred to 35 ml conical tubes; methanol insoluble pellets were washed 3 times by suspending in 1 ml of hot methanol and clarifying by centrifugation. The hot methanol washes were pooled with the MSF's and the pellets resuspended in 1 ml of D.I. water, covered with parafilm, and allowed to extract for 12 hours at room temperature.

Chlorophyll was extracted from the MSF using the ratio of MSF: anhydrous ethyl ether: D.I. water (1:1:1.2). The upper ether layer

was removed from the methanol-water fraction and brought to 10 ml with anhydrous ethyl ether. Total chlorophyll was determined according to the method of Strain and Svec (3) using the equation:

$$\mu\text{g Chl.} = 7.12 (A_{660}) + 16.8 (A_{642.5}) \times 10$$

After extraction for 12 hours in water, the methanol insoluble pellets were resuspended and clarified at 2500 RPM for 3 minutes and the supernatant fractions retained. The pellets were washed twice more with 1 ml of D.I. water and all the water fractions combined with the methanol-water fractions, then the total volumes recorded. A 0.1 ml aliquot of the methanol-water fraction was added to 10 ml of Aquasol-2 (New England Nuclear) liquid scintillation cocktail and radioactivity measured in a Beckman LS 100-C scintillation counter. Counting efficiency was determined to be 72 percent. The equation used to calculate the photosynthetic rate was:

$$\mu\text{g C/mg Chl/hr} = \frac{\text{DPM fixed}}{\text{DPM added}} \times 1.06 \times \frac{\mu\text{g } [^{12}\text{C}]}{\mu\text{g Chl}} \times 4000$$

D. Data analysis.

Interpretation of photosynthetic rate data was on the basis of percent inhibition from the control samples using the equation:

$$\% \text{ photosynthetic inhibition} = 1 - \frac{\mu\text{g C/mg Chl/hr (Mylar)}}{\mu\text{g C/mg Chl/hr (control)}} \times 100$$

The percentage of photosynthetic inhibition due to sensitization by a particular intensity of PAR was determined from the equation:

$$(\% \text{ inhibition UV-A+PAR}) - (\% \text{ inhibition UV-A}) = \begin{matrix} (\% \text{ inhibition} \\ \text{sensitization}) \end{matrix}$$

RESULTS

A. Prior studies.

Photorepair studies of UV-B induced, photosynthetic damage in Halophila engelmannii (4) led to the implication of UV-A as a potent photosynthetic inhibitor. A comparison of Mylar screened tissue samples (receiving UV-A and PAR) with dark controls from the experiments showed considerable photosynthetic inhibition as a result of the combined exposure. The addition of UV-B to the combined UV-A and PAR irradiation, by use of a Kodacel filter in place of Mylar, produced even greater photosynthetic inhibition at each PAR intensity. The increase in inhibition due to the addition of UV-B was not constant across the range of PAR intensities provided.

B. UV-A sensitivity.

Ultraviolet-A sensitivity was monitored in each experiment and calculated as the percent difference in photosynthetic rates of light controls and UV-A irradiated samples. During the test period, the seagrasses' sensitivities to UV-A varied somewhat (as expected) simply due to the variability inherent in field collections as compared to laboratory grown specimens.

Halophila showed a continued and significant sensitivity to UV-A during the test period with a photosynthetic inhibition mean value of 44 percent. Both Halodule and Syringodium had insignificant if any photosynthetic inhibition as a result of UV-A irradiation.

C. PAR influences on UV-A sensitivities.

Leaf tissues were exposed to UV-A and different PAR intensities (100-700 $\mu\text{E}/\text{m}^2/\text{sec}$, at 100 $\mu\text{E}/\text{m}^2/\text{sec}$ increments). The effect of a PAR intensity on UV-A sensitivity was corrected for any inherent UV-A intolerance prior to analysis (Methods, section D).

Figure 3 shows the extent of photosynthetic inhibition in Halophila as a function of PAR at constant UV-A irradiation. Considering a 44 percent inherent UV-A sensitivity in Halophila, a light compensation point to the UV-A induced damage of approximately 300 $\mu\text{E}/\text{m}^2/\text{sec}$ was obtained. Intensities of PAR above this point apparently increase the sensitivity of this species to UV-A. Below the compensation point a photorepair mechanism appears to be effective. The efficiency of this mechanism seems to decrease rapidly above 200 $\mu\text{E}/\text{m}^2/\text{sec}$. Figure 4 presents the degree of sensitization to UV-A by PAR in Halophila (on the basis of each tissue collection's sensitivity to UV-A rather than the mean value). This method produced a lower compensation point of about 220 $\mu\text{E}/\text{m}^2/\text{sec}$.

Halodule (Figure 5) showed quite a different response to UV-A in the presence of PAR. A bimodal interpretation was obtained with a sensitization to UV-A being induced at the high and low ends of the PAR intensity range provided. Maximum sensitization occurred at 200 $\mu\text{E}/\text{m}^2/\text{sec}$ and again at 600 $\mu\text{E}/\text{m}^2/\text{sec}$ of PAR. The middle range of PAR intensities (300-500 $\mu\text{E}/\text{m}^2/\text{sec}$) elicited no sensitization to UV-A. It is important to again note that Halodule suffered no apparent deleterious effects from UV-A irradiation in the absence of PAR.

Figure 3. Response of Halophila engelmannii to UV-A in terms of photosynthetic inhibition as a function of PAR intensity (closed points, samples response; solid line, mean response; dashed line, average photosynthetic inhibition produced by the UV-A irradiation in the absence of PAR).

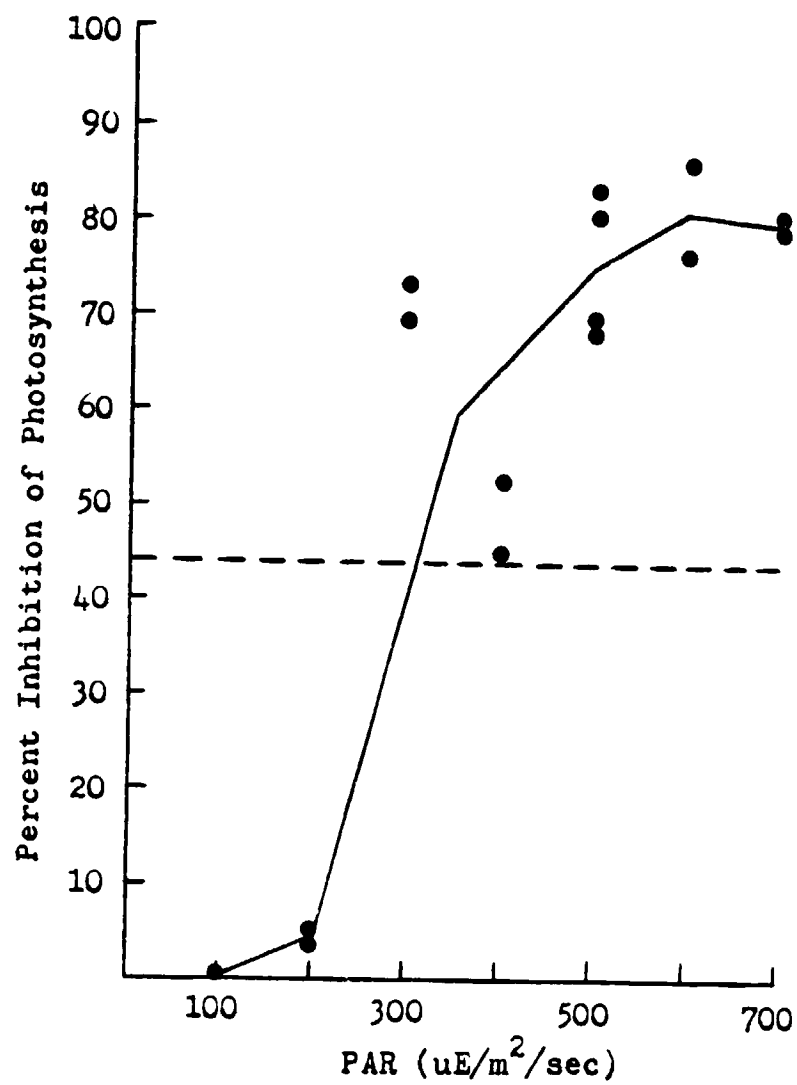


Figure 4. Sensitization to UV-A as a function of PAR intensity in Halophila engelmannii (closed points, samples response; solid line, mean response).

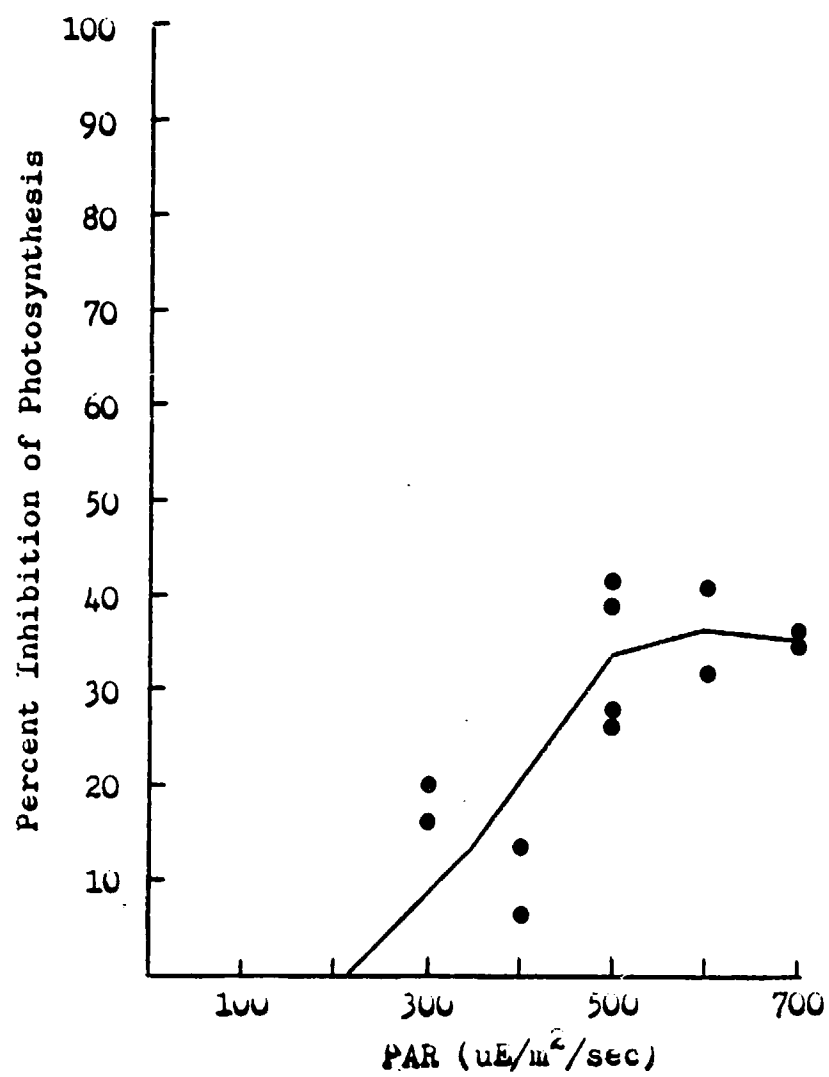
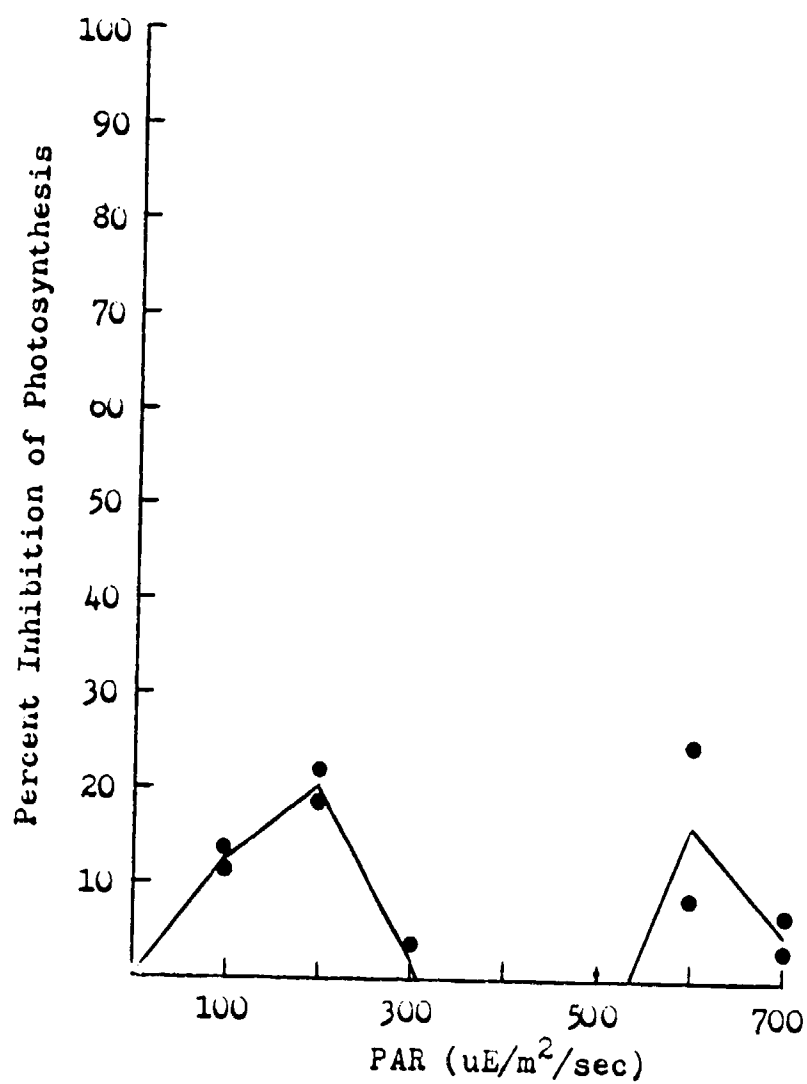
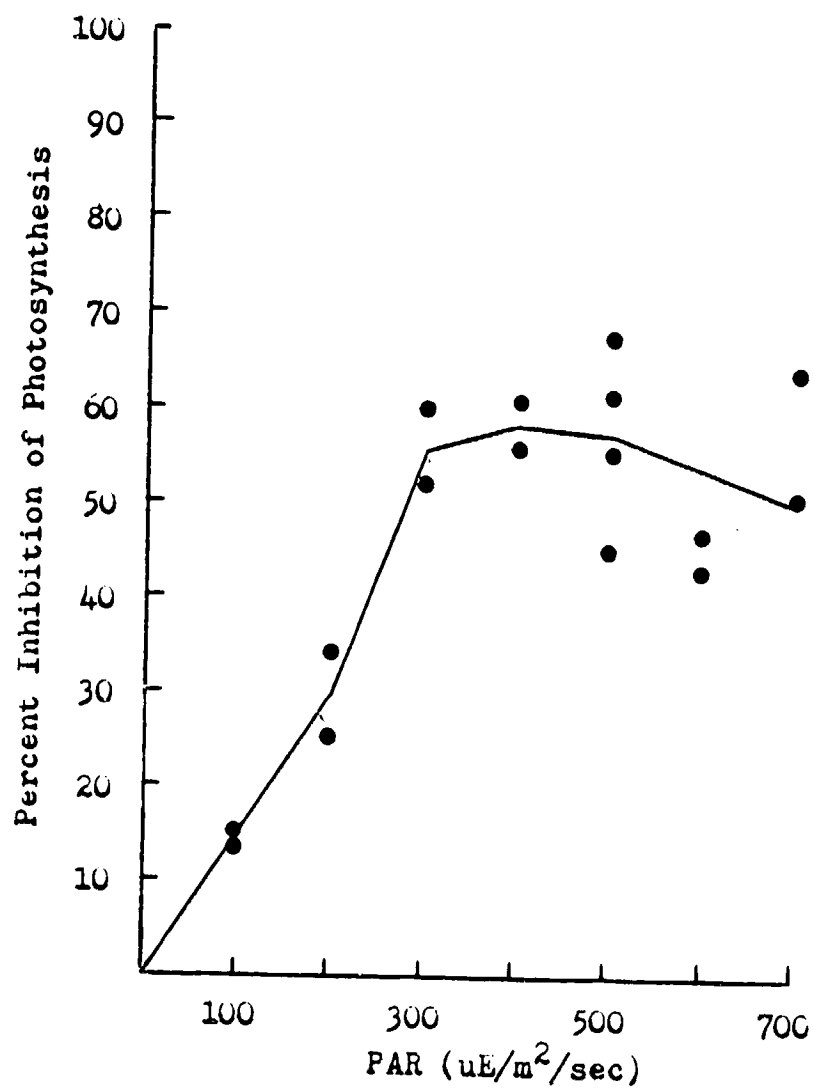


Figure 5. Sensitization of Halodule wrightii to UV-A as a function of PAR intensity (closed points, samples response; solid line, mean response).



Finally, Syringodium produced yet a third type of response (Figure 6). A rapid rise in sensitivity to UV-A was induced by providing a greater intensity of PAR. Sensitization reached a maximum above $300 \mu\text{E}/\text{m}^2/\text{sec}$ of PAR. As with Halodule, no inherent sensitivity to UV-A in the absence of PAR was observed in this species.

Figure 6. Sensitization of Syringodium filiforme to UV-A as a function of PAR intensity (closed points, samples response; solid line, mean response).



DISCUSSION

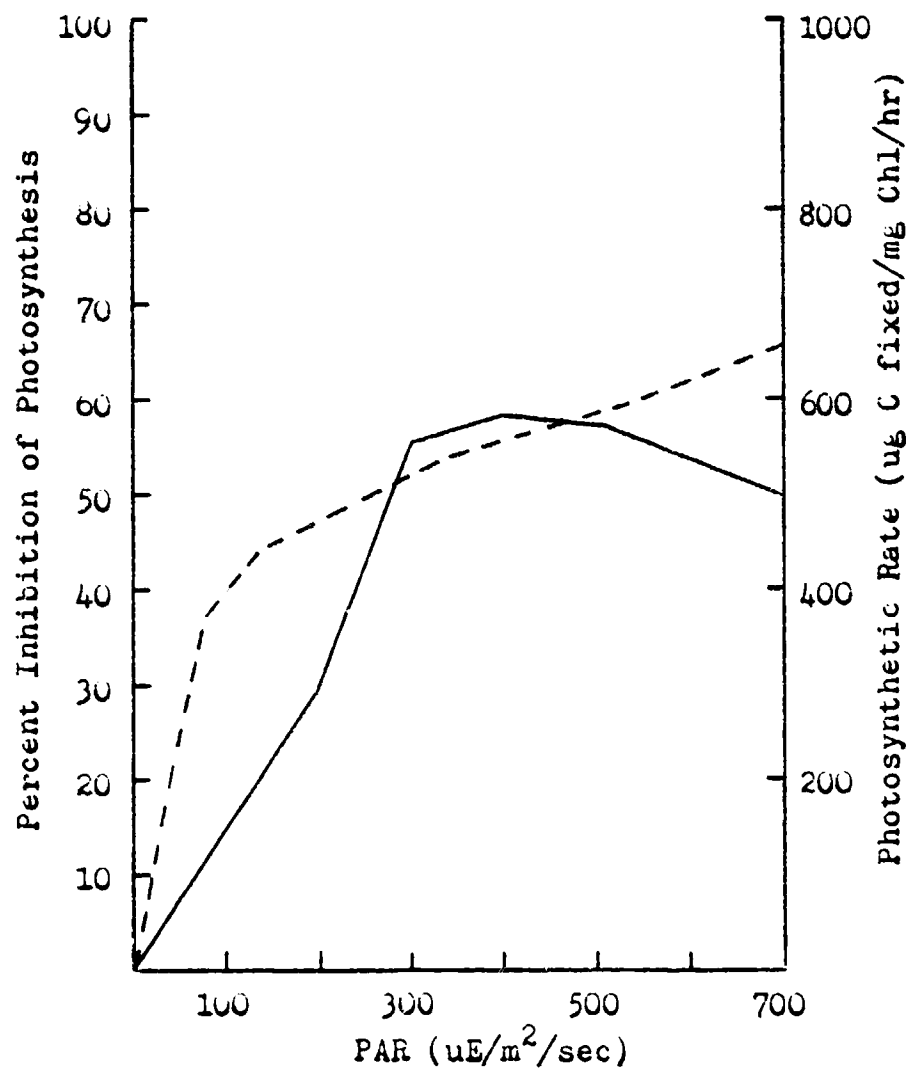
An intrinsic sensitivity to UV-A alone was apparent only in Halophila, while net photosynthesis in Halodule and Syringodium seemed unaffected by the level of UV-A provided. The sensitivity of Halophila to UV-A in the absence of PAR indicated the photosynthetic reaction need not be in operation for damage to occur. Ultraviolet-A apparently was able to penetrate the thin epidermal protection ionizing some photosynthetic component or inducing a degradative response nullifying a component(s) in the photosynthetic system. Further studies would be necessary to determine whether the site of action for UV-A was in the photosynthetic and/or supportive reactions. Halodule and Syringodium both showed an intrinsic tolerance to UV-A. This was not totally unexpected as both of these seagrasses were far more tolerant of the more energetic (and potentially destructive) UV-B than Halophila, making UV-A induced damage seem less likely. As UV-A is a normal component of the solar spectrum reaching the Earth's surface, the biochemical and morphological defenses to ultraviolet radiation may have been developed and targeted toward UV-A, operating less effectively (if at all) against UV-B; although adaptation may be occurring in these systems to handle increasing levels of UV-B.

The exposure of the seagrasses to UV-A in the presence of PAR produced a distincting response in each species. Syringodium became increasingly sensitized to UV-A irradiation as the PAR intensity increased. This suggested that either the photosynthetic mechanism must be operating, at least minimally, for UV-A to have an inhibitory effect

or there is a requirement for a PAR component to be present simultaneously with UV-A to elicit the inhibitory response. Evidence for the latter comes from the observation that photosynthesis by Syringodium is saturated at approximately $100 \mu\text{E}/\text{m}^2/\text{sec}$ yet the sensitization to UV-A by PAR increases to at least $300 \mu\text{E}/\text{m}^2/\text{sec}$ (Figure 7). At PAR intensities above $300 \mu\text{E}/\text{m}^2/\text{sec}$, it is possible that the UV-A component of the combined beam is limiting. In order to investigate this further, the UV-A intensity presented to the seagrass would have to be varied.

The response of Halodule to UV-A in the presence of PAR was similar to that of Syringodium. Halodule showed a sensitization to UV-A when this irradiation was combined with PAR exposure. In contrast to Syringodium, this species was not sensitized to UV-A by the entire range of PAR intensities provided. Intensities from $300\text{--}500 \mu\text{E}/\text{m}^2/\text{sec}$ did not facilitate a negative response to UV-A. The bimodal response (Results, section C) may be explained in several ways. If photosynthetic activity itself is the only requirement to induce a sensitivity to UV-A, it would appear a photorepair mechanism able to negate the UV-A effect became fully effective at PAR intensities of $300\text{--}500 \mu\text{E}/\text{m}^2/\text{sec}$. However if a combined beam of UV-A and PAR component is necessary for the inhibitory response, the situation becomes more complex. It is possible the PAR component of the combined UV-A+PAR beam is only "recognized" at certain intensities, in this case above $500 \mu\text{E}/\text{m}^2/\text{sec}$ or below $300 \mu\text{E}/\text{m}^2/\text{sec}$. At PAR intensities between these points a desensitization or lack of sensitization may occur. In addition, a photorepair mechanism to a combined beam inhibitor can not

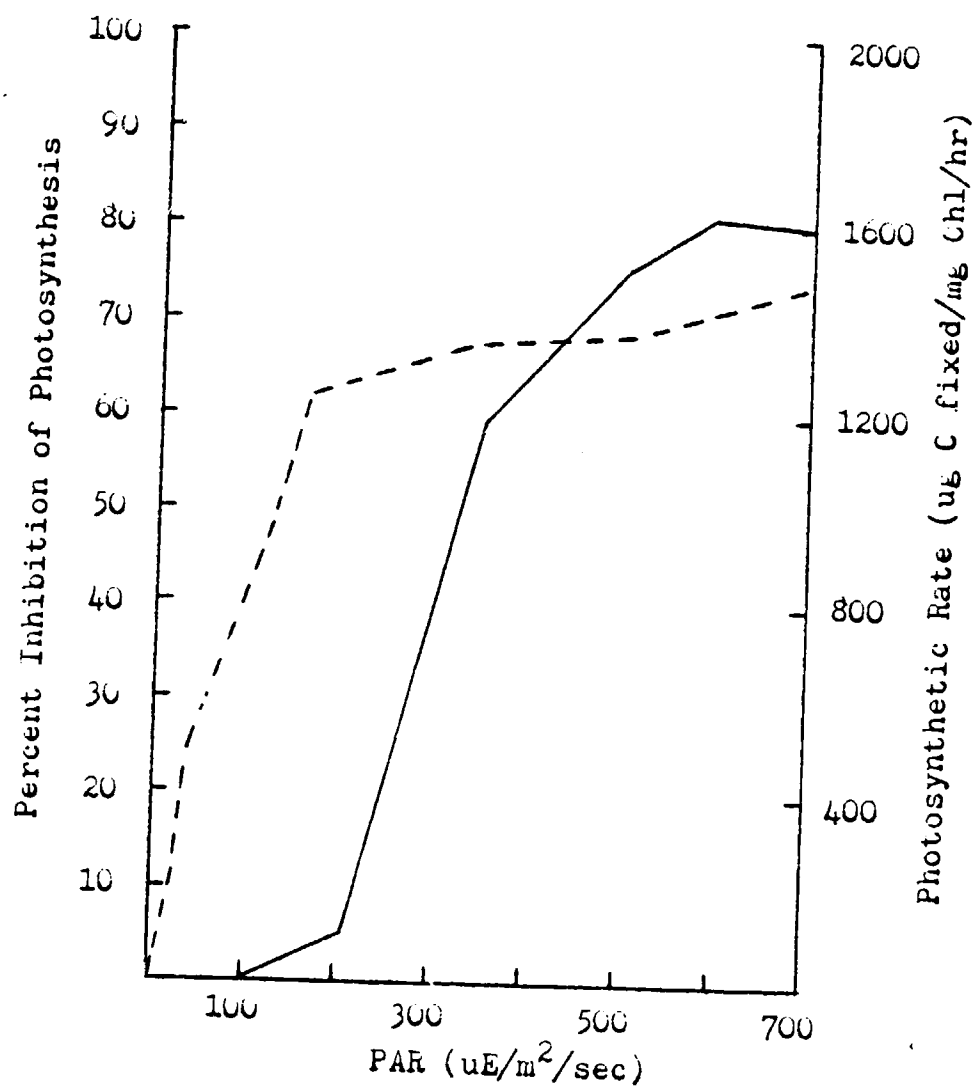
Figure 7. Photosynthetic saturation and UV-A sensitization in Syringodium
filiforme (solid line, mean sensitization response; dashed line, mean
photosynthetic rate).



be discounted. Another component of PAR (other than that of the combined beam) may activate a photorepair system which becomes fully effective when this particular component reaches an intensity reflected by total PAR intensities between $300 \mu\text{E}/\text{m}^2/\text{sec}$ and $500 \mu\text{E}/\text{m}^2/\text{sec}$. A first step in clarifying the situation would be to isolate the PAR component of the hypothetical UV-A+PAR combined beam. In any case, the range of PAR intensities in which UV-A failed to have an inhibitory effect may represent a fine-tuning of physiological processes to the prevalent PAR intensities experienced by Halodule in the field.

The response of Halophila to UV-A and PAR was unique among the three seagrasses in that photorepair to UV-A induced, photosynthetic inhibition and sensitization to UV-A by certain intensities of PAR were both clearly observed. An innate photosynthetic sensitivity to UV-A was seen for the first time and a PAR compensation point for UV-A induced damage was determined to be between 200 and $300 \mu\text{E}/\text{m}^2/\text{sec}$. As in Syringodium sensitization to UV-A increased at PAR intensities above those necessary to saturate the photosynthetic apparatus (Figure 8). This would tend to support a combined beam inhibition response. However sensitivity to UV-A in the absence of PAR indicated that photosynthesis need not be in operation for UV-A to cause damage. In addition the photorepair mechanism visible at low PAR intensities is not only able to negate the 44 percent photosynthetic inhibition by UV-A seen in this species, but also any sensitization by PAR which may have occurred. Perhaps the best explanation for these observations may be based on UV-A affecting both photosynthetic and supportive reactions. In the absence

Figure 8. Photosynthetic saturation and UV-A sensitization in Halophila engelmannii (solid line, mean sensitization response; dashed line, mean photosynthetic rate).



of PAR (no photosynthetic activity) supportive reactions may be inhibited by UV-A or essential substances ionized so in subsequent photosynthetic rate determinations an inhibition was observed. When photosynthesis is proceeding at low intensities of PAR (below 200-300 $\mu\text{E}/\text{m}^2/\text{sec}$) a photorepair mechanism may prevent damage from overpowering the photosynthetic reaction and mask damage in nonphotosynthetic reactions. Whatever sensitization to UV-A by PAR may be counteracted by the photorepair mechanism until the intensity of the PAR component in the combined beam becomes sufficient to increase the sensitivity to UV-A above the level that photorepair can compensate for (this assumes the PAR portion of the combined beam is limiting). If sensitization to UV-A and photorepair occur separately and simultaneously, the degree of sensitization by PAR seen in Figure 4 is apparent rather than actual (it must also be assumed that photorepair is operational at PAR intensities above the compensation point). Further studies would be necessary to clarify the situation.

The sensitivity of Halophila to UV-A in the presence and absence of PAR may act as one factor limiting the upper distribution of the species. Pure stands of this seagrass were not seen in waters less than 0.5 m in depth. In shallower areas this seagrass was always found in close association with Halodule and/or Syringodium, lying in their "shadow". Detrital cover and epiphytic growth on Halophila was also greater in these shallow areas. The shielding action of these materials and organisms may reduce the amount of UV-A penetrating to the leaf tissues. The reduction in photosynthetic activity due to an accompanying blockage of PAR is probably of little consequence in all but the most

turbid circumstances.

Syringodium gave no indication of a photorepair capability to deal with UV-A effects. Apparently, as with UV-B, this species relies on morphological and environmental defenses to avoid UV-A induced, photosynthetic damage. Morphologically, the bulk of the photosynthetic tissue is protected by a thick epidermal layer. The environment provides additional protection simply due to the rapid attenuation of UV-A in the water column relative to PAR. This is of particular relevance as Syringodium blade growth occurs from the base rather than the tip; the actively growing portion of the seagrass may in this manner be protected from UV-A. Epiphytic growth undoubtedly also plays a role (whether or not by design) in preventing UV-A damage by physically shielding the seagrass. Syringodium often takes on a "cattail-like" appearance during epiphytic blooms, the upper portion of the seagrass blade covered by a thick mat of epiphytes.

Halodule may also take advantage of environmental and epiphytic characteristics to augment its apparent photorepair capability. In this species, and Halophila as well, epiphytic and detrital deposits may not only shield the seagrass from some UV-A but reduce the penetrant PAR intensity to levels where photorepair is capable of compensating for any UV-A sensitization.

As in many investigations, this study has perhaps raised more questions than it has answered. Unfortunately equipment able to measure in situ and laboratory levels of UV-A was unavailable (Methods, section C) which makes more extensive and definitive interpretation of

experimental data hazardous. Estimation of the current environmental significance of UV-A and UV-B without in situ measurements of UV-A could only be made empirically. On the basis of the rapid attenuation of UV-B in the water column, the seagrasses' different sensitivities to UV-A and UV-B, and the sensitization to UV-A in the presence of PAR it appears UV-B decreases in significance from Halodule to Syringodium and finally Halophila. Ultraviolet-A seems somewhat the reverse, increasing in importance from Halodule to Syringodium and Halophila. In terms of biomass and systematic importance, UV-B would appear the more significant if only due to the relative abundance of the species (Halodule and Syringodium being far more abundant than Halophila).

CONCLUSIONS

The responses of the three seagrasses (Halophila engelmannii, Halodule wrightii, and Syringodium filiforme) to UV-A in the presence or absence of PAR were distincting and diverse. Halophila was the only species to be intrinsically sensitive to UV-A. In the presence of PAR a dual response was obtained, below 300 $\mu\text{E}/\text{m}^2/\text{sec}$ a photorepair response was observed while above this PAR intensity a sensitization to UV-A occurred. Syringodium, while not photosynthetically inhibited by UV-A irradiation, was sensitized to UV-A when PAR was provided simultaneously. Sensitization to UV-A increased with each 100 $\mu\text{E}/\text{m}^2/\text{sec}$ PAR increase until a maximum sensitivity was reached at 300 $\mu\text{E}/\text{m}^2/\text{sec}$. Halodule was also insensitive to UV-A in the absence of PAR, however unlike Syringodium, certain PAR intensities failed to sensitize the seagrass to UV-A while yet others did elicit such a response. In the cases of both Halophila and Halodule the PAR intensities which either supported photorepair or failed to cause a sensitization to UV-A appeared to represent an adaptation to the dominant PAR intensities these species encounter in the natural system.

In regard to the significance of UV-A and UV-B in the natural system it seems (on the basis of the enclosed and previous observations) that UV-B is of greater current environmental importance to the seagrass communities of the Florida east coast.

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